

Studies Concerning the Reaction of Barley
to Two Undescribed Physiologic Races
of Barley Mildew, Erysiphe Graminis
Hordei Marchal

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STUDIES CONCERNING THE REACTION OF BARLEY TO TWO UNDESCRIBED PHYSIOLOGIC RACES OF BARLEY MILDEW, *ERYSIPHE GRAMINIS HORDEI* MARCHAL¹

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INTRODUCTION

Salmon (26, 27) lists 59 species in 26 genera of grasses as hosts of *Erysiphe graminis* DC. Marchal (17) was the first to show that this species contained several “*formes spécialisées*”, or physiologic varieties, differentiated by their host specialization. From further investigations by both Salmon (28, 29, 30, 31) and Reed (19, 20, 21, 23), it is evident that different varieties occur on each of the cereals, oats, barley, rye, and wheat. Moreover, distinct varieties occur on each of the following genera of grasses: *Agropyron*, *Bromus*, *Dactylis*, and *Poa*. In general, each variety is closely confined to species of a single genus. Two of the varieties, *Hordei* and *Tritici*, are known to contain physiologic races. Mains and Dietz (15) first demonstrated this for the *Hordei* variety, and Mains (14) has shown this to be true for the *Tritici* variety. The present investigation is limited to 2 hitherto undescribed physiologic races of the *Hordei* variety.

Genetical studies concerning the resistance of barley to powdery mildew are few. In 1907, Biffen (1) studied a cross between a resistant and a susceptible variety. Recent genetical investigations are those of Dietz (5), Honecker (8, 9), and Briggs (2), each of whom used different physiologic races of *Erysiphe graminis hordei* as inoculum. Briggs also studied mildew resistance in relation to other factors.

MATERIALS AND METHODS OF STUDY

Seed of the barley species, varieties, and crosses was furnished by E. B. Mains. The study of crosses was started with the F₂. The mildew was obtained from infected barley growing in the greenhouses at the Botanical Gardens of the University of Michigan.

In studies of the seedling reactions, approximately 10 to 15 seeds of each of the varieties to be tested were planted in 3½ inch pots on the greenhouse

¹ Papers from the Department of Botany and Herbarium of the University of Michigan No. 570.

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bench. When the first two or three leaves were showing the plants were sprayed with a fine mist of water and then were inoculated by shaking heavily mildewed plants over them. A uniform distribution of conidia was thus obtained on all leaves. The plants were then covered with wet muslin suspended on wires over the pots. When this was done in late afternoon a fine dew occurred on the leaves the next morning. At this time the plants were often reinoculated, thus insuring a more abundant infection. The wet cloth was removed at the end of about 24 hours from the time of first covering. In warm, sunny weather it covered the plants only at night because of the excessively high day temperature.

In the winter, when the temperature was more uniform in the greenhouse, 65° to 75° F. during the day and 55° to 65° at night, good infection was obtained merely by shaking heavily mildewed plants over the varieties to be inoculated without covering the plants with wet cloth. The inoculum was obtained from seedling plants of highly susceptible varieties, such as Oderbrucker C. I. 940.

Notes were taken about 10 to 20 days after inoculation, when the mildew had reached its fullest development. As the time approached for taking such notes the plants were no longer watered from above. In this way, washing of the spores from the leaves was considerably reduced and readings were facilitated.

Five types of reaction of the host varieties were recognized, similar to those distinguished by Mains and Dietz (15), Dietz (5), and Mains and Martini (16) in their studies of the powdery mildew of barley. These types are as follows:

0. Highly resistant. Macroscopically, no mildew evident; chlorotic or necrotic spots, or smaller areas appearing as white flecks may be developed by some varieties.

1. Very resistant. Slight to moderate development of mycelium evident macroscopically, but with little or no sporulation; chlorotic or necrotic spots, or brownish areas developed by some varieties.

2. Moderately resistant. Moderate to abundant development of mycelium accompanied by a slight production of conidia; chlorotic or necrotic spots formed by some varieties.

3. Moderately susceptible. Moderate to abundant development of mycelium accompanied by moderate sporulation.

4. Very susceptible. Abundant mycelium developed, accompanied by abundant sporulation.

The "X" type of reaction often encountered by workers with cereal rusts was seldom found in tests of barley reacting to pure physiologic races of the mildew. This is essentially a heterogeneous type of infection in which several, if not all, of the types of infection from 0 to 4 are found on the same

leaf. Plants encountered in crosses between susceptible and resistant varieties that gave this or a type 2-3 reaction are listed in the present paper as "intermediate" in reaction.

A mixture of several races usually is indicated by one or more of the differential varieties giving two or more types of reaction at the same time, much as one encounters in the "X" type of reaction. In such instances pure cultures of the races present may be obtained by resort to one of several methods. Mains (12) and Newton and Johnson (18) have given an excellent discussion of the separation of individual races from cultures containing several physiologic races in certain of the cereal rusts. Much of the technique that they describe is applicable also to powdery mildew of barley.

In the present study resort was made constantly to single pustules in order to obtain pure cultures of the races under consideration. Seedlings known to be susceptible to several races were placed on the greenhouse bench, where mildewed barley also was present. Such healthy seedling plants usually were placed 10 to 30 feet from the mildewed plants and exposed for a day to conidia that were in the air of the room. They were then removed to a compartment where there was no mildew. After the usual period of incubation signs of infection appeared on the leaves as white flecks. As the inoculation had been scattered, plants with a single white fleck of mildew could be easily isolated. If other leaves of the plant also were flecked, they were removed, leaving in every case a single white fleck or mildew pustule to a plant. These selected plants were placed in separate moist chambers or compartments and kept from further exposure to conidia. When a single pustule began to sporulate, transfers of the conidia were made with the moistened blade of a spatula to other healthy susceptible plants. The mildew was then multiplied.

REACTION OF BARLEY TO PHYSIOLOGIC RACES 6 AND 7 OF *ERYSIPHE GRAMINIS HORDEI*

The results presented in this and the following section were obtained during investigations conducted during the winter (November-March) and spring (April-May), 1933-1934, and the winter of 1934-1935 in greenhouse studies. In winter tests, a day temperature of 65° to 75° F., and a night temperature of 55° to 65° was maintained. In the spring the temperature occasionally went as high as 90° during the day.

Two physiologic races were isolated that did not agree with those previously described. These are designated as physiologic races 6 and 7.

Differential Host Varieties for the Identification of Seven Physiologic Races of Barley Mildew

Mains and Dietz (15) used the reactions of 4 barley varieties, Black Hull-less C. I. 666, Goldfoil C. I. 928, Nepal C. I. 595, and Peruvian C. I. 935, in

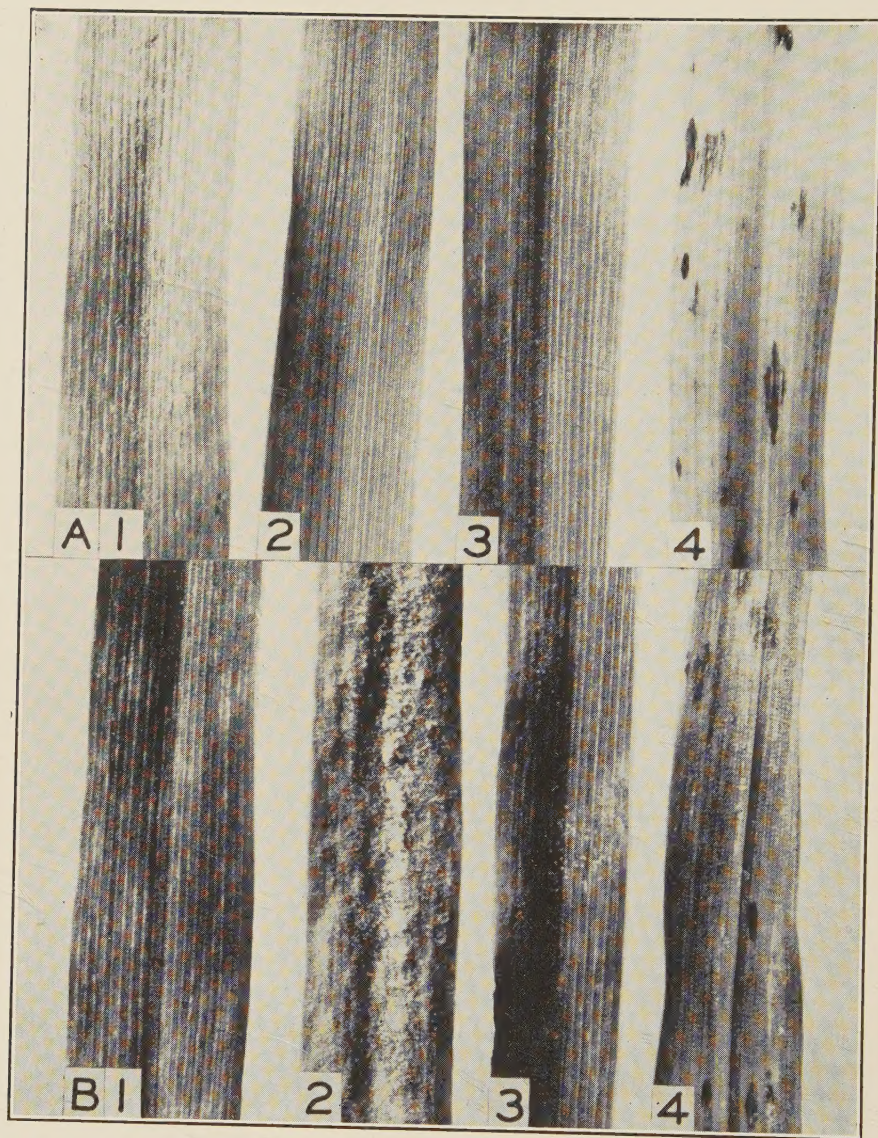


FIG. 1. Reaction of seedling leaves of four differential varieties of barley to two physiologic races of *Erysiphe graminis hordei*. $\times 3$. A. Four varieties inoculated with p. r. 6. (1) Nepal C. I. 595, type 1, very resistant, slight development of mycelium. (2) Goldfoil C. I. 928, type 0, highly resistant. (3) Peruvian C. I. 935, type 0, highly resistant. (4) Black Hull-less C. I. 666, type 0, highly resistant with conspicuous necrotic spots. B. Same four varieties inoculated with p. r. 7. (1) Type 1-, very resistant, very slight development of mildew. (2) Type 3+, very susceptible, abundant development of mycelium and moderate sporulation. (3) Type 1, very resistant, slight development of mycelium. (4) Type 1-, very slight development of mycelium, definite necrotic spots.

order to separate the 5 physiologic races of powdery mildew they isolated. It is necessary to add Heil's Hanna 3 C. I. 682 to this list of differentials in order to separate races 6 and 1. The reactions of these 5 varieties to the 7 physiologic races are presented in table 1. Figure 1 illustrates the reactions of 4 of the differential varieties to races 6 and 7. No decided changes in reaction to either race 6 or 7 were noted between winter and spring tests, under the conditions of this study. Since no tests were conducted during the summer, in either greenhouse or field, it is not known whether these reactions will be changed under such conditions.

TABLE 1.—*Reactions of five differential varieties of barley in the seedling stage to seven physiologic races of Erysiphe graminis hordei*^a

Variety	C. I. ^b No.	Type of reaction to physiologic race						
		1	2	3	4	5	6	7
Black Hull-less	666	0-2	1-2	3+	4	3	0-2	0-1
Goldfoil	928	0	0	0	0	4	0	3-4
Heil's Hanna 3 ...	682	1-2	4	4	3-4	4	3-4	3-4
Nepal	595	1-2	4	4	4	4	0-1+	0-1+
Peruvian	935	0-1	1	3-4	1	4	0-1+	0-1+

^a The data for the reactions of these varieties to races 1 to 5 inclusive were obtained from Mains and Dietz (15, p. 233).

^b Accession number of the Division of Cereal Crops and Diseases, United States Department of Agriculture.

Reactions of Seedling Plants

Both physiologic races 6 and 7 were tested on seedlings of a number of varieties several times during the winter and spring, under the differing environmental conditions then prevalent. In general, most of the varieties reacted to race 6 much as they did to race 7 (Table 2). However, two varieties, Goldfoil C. I. 928 (Fig. 1, A2 and B2) and Hanna C. I. 906 gave reactions that differed decidedly. Both varieties were extremely resistant to race 6, giving a 0 reaction. To race 7 they were very susceptible, giving reactions of 3 or 4.

A number of varieties were extremely resistant to both races in winter and spring tests, for the most part consistently giving 0 reactions. Such varieties were Albacaete C. I. 1128, Arlington C. I. 702, Chevron C. I. 1111, Chinerme C. I. 1079, Duplex C. I. 2433, Monte Cristo C. I. 1017, C. I. 2444, M756, M757, and Psaknon B81. All, except Psaknon B81, remained green and healthy with little or no flecking, no chlorosis, and no necrosis. Psaknon showed occasional flecking and a slight browning of the leaf tissue.

A larger number of varieties were classed as very resistant, yet varying in reaction from 0 to 1. With Chilean C C. I. 1432, Chilean D C. I.

1433, Coast C. I. 276, Peruvian C. I. 1131, C. I. 1080, C. I. 2416, and Orge Fourragère B102, there was a sparse development of mycelium occasionally with a slight brown discoloration of the leaf surface under the mycelium. Sometimes this was accompanied by a slight flecking, but never with any decided necrosis of host tissue. Other varieties, such as Kwan C. I. 1016, Sulu C. I. 1022, C. I. 1021, and No. 22 B69, also gave 0 to 1 reactions, but with a conspicuous necrosis of leaf tissue. Necrotic areas several millimeters in length often were produced. In the center of some of these a little tuft of mildew mycelium occasionally was observed. Black Hull-less C. I. 666 (Fig. 1, A4 and B4) and Minsturdi M784 also were resistant, with necrosis accompanying the slight development of mycelium.

Several other varieties, classed as very resistant, varied slightly, depending on whether the tests were conducted in winter or spring. Nepal C. I. 475 and Arequipa C. I. 1256, which gave reactions as high as 2 to physiologic race 6 during the winter, gave a type-1 reaction in the spring. Juliaca C. I. 1114 varied in the winter readings, sometimes giving a type-1 reaction to race 6 and at other times as high as 3. In the spring the reactions were never higher than 1. Peru C. I. 653 sometimes gave a type-2 reaction in the winter, while in the spring this variety was slightly more resistant. The reverse, that varieties resistant in the winter were less resistant in the spring, was seldom true.

Many varieties were noted as susceptible to both races during winter and spring. In the winter some of these were moderately or highly susceptible, giving type-3 or 4 reactions, while in the spring, they were only moderately susceptible. Featherston C. I. 1120, Hooded Spring C. I. 716, and Manchuria B44 are examples. Several varieties that gave type-3 or 4 reactions in the winter gave readings as low as 2+ or 2 in the spring. Bohemia C. I. 204 was occasionally slightly more susceptible in spring than in winter. Horsford C. I. 507 and Malting C. I. 1129 are typical of the many varieties that gave type-3 or 4 reactions in both winter and spring tests to both physiologic races.

The reactions of Goldfoil C. I. 928, Hanna C. I. 906, Bohemia C. I. 204 and Palestine C. I. 939 to races 6 and 7 were interesting because these were strains of the same botanical variety of *Hordeum distichon*. Bohemia was very susceptible to both races, Palestine was very resistant to both races, but Hanna and Goldfoil were highly resistant to race 6 and very susceptible to race 7.

On seedling leaves of susceptible plants so-called "green islands" were sometimes observed, especially during the spring tests. The leaf tissue under and immediately adjoining the mildew pustules remained green, while the remainder of the leaf became yellow. In the winter, infected leaves of susceptible varieties succumbed more quickly to the mildew, and "green islands" were seldom noted.

TABLE 2.—*Reaction of barley varieties to two physiologic races of powdery mildew, Erysiphe graminis hordei, in greenhouse studies*

Variety	Accession No. ^a	Type of reaction of					
		seedling plants				adult plants	
		to				to	
		P. r. 6		P. r. 7		P. r. 6	
		Winter	Spring	Winter	Spring	Winter	Spring
Abyssinia	362	1	0-1	1	1	1	0
Abyssinian	1243	1	0-1	1+	1	1	0-1
Albacaete	1128	0-1	0	0	0	1	0
Arequipa	1256	1-2	1	1+	1	1-2	0
Arlington	702	0	0	0-1	0	0-1	0
Black Hull-less	666	0-2	0-1	0-1	1-	0-1	0
Black Hull-less	1032	0-2	1-1+	1-2	1-2	0-1	
Blackhull	878	1	1-	0-1	1	0-1	0
Bohemia	204	3-3+	2-4	3+	3-4	2-3	
Bolivia	1257	1	0-1	0-1+	1	1	0
Callas	2440	2	1-2	3		0-1	0
Chevron	1111	0-1	0	0	0	0	0
Chilean C	1432	0-1	0-1	0	0-1	0	0
Chilean D	1433	0-1	0-1	0	0-1	0	0
Chinerme	1079	0	0	0	0	0	0
Coast	276	0-1	0-1	0-1	0-1	0	
Common Chile	663	1	0	0-1	0-1	0-1	
Consul	1061	1-	1-	1	1-	0-1	0
Duplex	2433	0	0	0	0	0	0
Featherston	1120	3-4	3	4	3	3-4	1+
Goldfoil	928	0	0	3-4	3+	0	0
Hanna	906	0	0	3-4	3+	0	0
Hanna	966	1	1	1	1-	1-	
Heil's Hanna 3	682	3-4	3	3-4	3+	2-3	0
Hooded Spring	716	3-4	3	3-4	3	4	0-1
Horsford	507	3-4	3	3-4	3	3	0
Horsford	610	3-4	3-4	3-4	3-	3	0
Horsford	877	4-	4-	3-4	3	3-4	2-
Juliaea	1114	1-3	1	1-3	1-2	1-2	0
Kwan	1016	0-1	0-1	0-1	0-1	0-1	0
Lion	923	1-2	1-2	1-2+	1-	1	0
Luth	972	0-1	0-1	0-1	0-1	0-1	0
Lynch	919	0-1	0	0-1+	0	0	0
Malting	1129	3-4	3	4	3	3-4	0-2+
Manchuria	2330	3-4	3-4	4	3	4	0-2
Mecknos Moroc	1379	3-3+	2+	3-4		2-3	0-1
Monte Cristo	1017	0	0	0	0	0	0
Nepal	475	1-2	1	1	1	1	0
Nepal	595	0-1+	1	0-1+	1	0-1	0
Oderbrucker	940	3-4	2-3	3-4	3	3-4	1-2
Oderbrucker	957	3	3-	4		4	1-2
Palestine	939	0-1	1-	1	1	1	0
Peru	653	1-2	0-1	1-1+	1-	0-1	
Peruvian	935	0-1+	1-	0-1+	0-1	1	0-1
Peruvian	1131	0-1	0-1	1	0-1	1	0
Purple Nepal	1373	1-	1-	1	1-	0-1	0
Quinn	1024	3	3	4		3+	1-2
Sulu	1022	0-1	0	0-1	0	0-1	0-1
.....	1021	0-1	0-1	0	0-1	0-1	0
Turkestan	711	0-1	0-1	1	1-	1	0

TABLE 2.—(Continued)

Variety	Accession No. ^a	Type of reaction of					
		seedling plants				adult plants	
		to				to	
		P. r. 6		P. r. 7		P. r. 6	
		Winter	Spring	Winter	Spring	Winter	Spring
Turkestan	1080	0-1	0-1	0-1	0-1	1	0
	1347	3-3+	2-3	3	3	3	0
	2329	1	1	1	0-1		0
	2416	1	0-1	0-1	0-1	1	
	2444	0	0	0	0	0	
California Feed	B59	3	3	3-4	2	2	
Coast	B121	1	1	1+	1-	1	
Colsess	B97	1	1	1+	1-		
Lion	B33	3-4	2-4	3-4	3-	2+	
Loeride	B86	0-1	0-1	0-2	1+	1-2	
Manchuria Sel. C163	B40	3-4	3-4	3-4	3	3-4	
Manchuria Sel. C164	B41	3-4	3-	3-4	3	3	
Manchuria Minn. 184	B43	3-4	3	3-4	3	3	
Manchuria	B44	3-4	3	3-4	3	3-4	
O. A. C. 21	B61	3-4	2-4	3-4	3	3-4	
Orge Fourragère	B102	0-1	1	1	1	0-1	
Orge 4th	B100	3-4	3-4	4-	3-	2	
Orge 14 J	B101	3-4	2-4	3-4	1-3	1+	
Psaknon	B81	0	0-1	0	0	0	
Sahara	B95	1	1	1-2	1-	1-1+	
Smooth Awn × Manchuria...	B35	3-4	3	3-4	2+	3-4	
Smooth Awn × Manchuria...	B36	3-4	3	4	2	3	
Smooth Awn × Manchuria...	B37	3-4	2-3	4	3	3	
Smooth Awn × Manchuria...	B38	3-4	2-3	4	3	3-4	
Virginia Hooded	B6	3-4	3-4	4	3	2-3	
No. 22	B69	0-1	0-1	0	0-1	1	
No. 305	B85	1-3	1-3	2-3	1-2	1	
Glabron	M781	3-4	3-	3	3	3-4	
Manchuria	M785	3-4	2-3	3+	3-	3-4	
Minsturdi	M784	0-1	1	1	1	1	0
Sacramento	M777	0-1	1-	0-1	1-	0-1	
Spartan	M788	3	3-	3-4	3	3	
Svansota	M786	3-4	2-3	3-4	3	3	0
	M756	0	0	0	0	0	
	M757	0	0	0	0	0	

^a Numbers in this column *not* preceded by a letter are C. I. numbers of the Division of Cereal Crops and Diseases, United States Department of Agriculture. Numbers preceded by B are the numbers under which the varieties were received from W. L. Waterhouse (13, p. 880). Numbers preceded by M are accession numbers of E. B. Mains.

Reactions of Adult Plants

Adult plants of certain varieties also were inoculated at two seasons of the year in greenhouse studies. In these tests physiologic race 6 was used for inoculum.

The reactions of 83 varieties were obtained in the winter investigations (Table 2). Readings were made in March when the plants were in the late

shooting or heading stages. Varieties, resistant in the seedling stage, were resistant also in the adult stage. Necrosis of leaf tissue, very prevalent on seedling plants of such varieties as Kwan C. I. 1016, Sulu C. I. 1022, and Minsturdi M784, was much reduced or entirely lacking. Instead, only a browning of the host tissue was apparent. Chlorosis and flecking were more pronounced on some varieties than in seedling tests. Almost all varieties, moderately or highly susceptible as seedlings, were equally susceptible in the adult stage. On many varieties, such as Malting C. I. 1129 and several strains of Manchuria, which gave a type-3 or 4 reaction, the mildew was abundant on leaf sheaths and beards, as well as on the leaf blades. In many instances the heads were well past flowering, yet the beards were heavily mildewed. A few varieties, susceptible as seedlings, were slightly more resistant in the adult stage, giving reactions of type-2 to 3. Mecknos Maroc C. I. 1379 is an example. It was further noted that heavily mildewed plants were delayed in coming to full maturity, and the seeds in the heads were greatly reduced in number.

In another experiment, conducted with a limited number of adult plants, readings were made in November and early December, a mixture of races

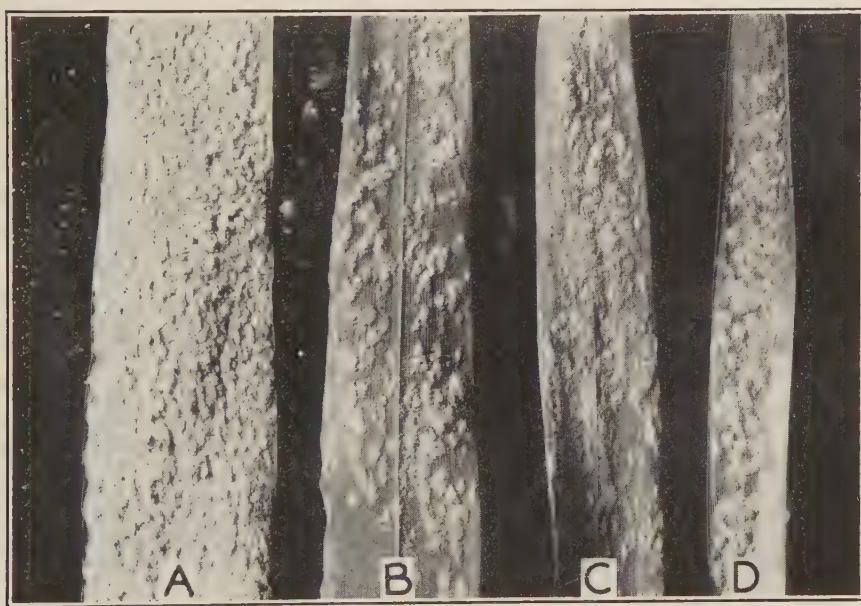


FIG. 2. Upper leaves of adult plants of four susceptible varieties of barley inoculated in winter tests in greenhouse studies with a mixture of races 6 and 7 of powdery mildew. $\times 1$. A. Flag leaf of Manchuria M785, type 4. B. Oderbrucker C. I. 940, third leaf from top of plant, type 3. C. Virginia Hooded B6, third leaf from top of plant, type 3. D. Smooth Awn $\times$ Manchuria B36, flag leaf, type 3.

6 and 7 being used for inoculum. Results were obtained that again indicated that, given certain environmental conditions, adult barley plants are as susceptible to mildew as are seedling plants of the same varieties (Fig. 2).

In the spring series most of the varieties were in the shooting or heading stages when exposed to mildew conidia. Readings were made during the first 2 weeks of May, and the data in table 2 records the reaction noted at the time of full expression of the mildew infection. As shown in table 2, all the 48 adult varieties tested in the spring were more or less resistant. Varieties, highly resistant in the seedling stage, were equally resistant in the adult stage. Some of the varieties, showing type-3 or 4 reactions as seedlings, were highly resistant. Horsford C. I. 610 is typical. Others, such as Oderbrucker C. I. 940 and Quinn C. I. 1024, which were susceptible in the seedling stage, gave reactions ranging from 1 to 2 on the upper leaves. A slight chlorosis of leaf tissue accompanied the slight to moderate development of mycelium on many of these varieties.

Reactions of Wild Species of *Hordeum*

The following wild species of *Hordeum* were used in these experiments: Seven collections of *Hordeum murinum* L., 6 collections of *H. gussoneanum* Parl., 2 collections of *H. nodosum* L., and single collections of *H. pusillum* Nutt. and *H. jubatum* L.

The plants were first inoculated in the usual manner with physiologic race 6 in winter of 1934-1935, when they were in the 3-leaf stage. For a period of 4 weeks following this first inoculation they were constantly exposed to inoculum from heavily mildewed barley varieties that were nearby on the greenhouse bench. At no time during this period did any signs or symptoms of the disease appear on the wild species of *Hordeum* thus inoculated.

INHERITANCE OF RESISTANCE

Svansota M786 $\times$ Hanna C. I. 906

Both Svansota and Hanna are 2-rowed barleys. In the seedling stage in the winter, Svansota is very susceptible (type 3-4) to race 6, whereas Hanna C. I. 906 is highly resistant (type 0). The reactions of the F_2 seedlings were obtained in studies made in December, 1933. F_3 progeny tests were conducted in February, 1935.

In the F_2 test 98 plants gave a type-4 reaction, 228 a reaction of 1 or 1-2, and 118 a reaction of 0. This approximates a 1 : 2 : 1 ratio of 111 : 222 : 111, the deviations for the 3 classes being - 13, 6, 7 and Dev. $\div$ P.E. 2.11, 0.84, 1.14.

F_3 progeny tests were made of 25 to 35 plants derived from each of 262 of the F_2 plants. Forty-eight susceptible F_2 plants proved to be homozygous for susceptibility. Sixty-five of the 67 individuals, classed as highly resistant (type 0) in the F_2 , bred true for high resistance. The progenies

in the other two lines segregated. The misclassification of these F_2 plants is not surprising when the closeness of reaction of the two resistant classes is considered. Ten of the 147 F_2 plants, classified as type 1 or 1-2, gave F_3 progenies with only 0 reaction. The plants in the remaining 137 lines segregated.

Of 3983 F_3 plants from the 139 segregating lines 1039 gave a type-4 reaction, 2011 a reaction of 1 or 1-2, and 933 a reaction of 0. This approximates a 1:2:1 ratio of 995.75:1991.50:995.75, the deviations for the three classes being 43.25, 19.50, -62.75 and $\text{Dev.} \div \text{P.E.}$ 2.34, 0.92, 3.40.

The results obtained in the F_2 and verified by tests of F_3 lines indicate that the resistance of Hanna C. I. 906 to physiologic race 6 in the seedling stage is due to a single Mendelian factor. Apparently, the marked resistance of Hanna is not completely dominant. Heterozygous individuals, although resistant, are less so than the Hanna parent.

Featherston C. I. 1118 $\times$ Goldfoil C. I. 928

Featherston is a 6-row and Goldfoil a 2-row variety. Goldfoil is highly resistant (type 0) to race 6. The reaction of Featherston to race 6 was not obtained. The reactions of F_2 seedling plants were obtained in May, 1934, and those of F_3 lines in February, 1935. Physiologic race 6 of the mildew was used for inoculum.

In the F_2 test 37 plants gave a type-3 or 4 reaction, 70 a reaction of 2-3, and 38 a reaction of 0, 1, or 2. This closely approximates a 1 susceptible:2 intermediate:1 resistant ratio of 36.25:72.50:36.25, the deviations for the 3 classes being 0.75, -2.50, 1.75 and $\text{Dev.} \div \text{P.E.}$ 0.21, 0.62, 0.50.

Tests of approximately 25 to 35 F_3 plants from seed of each of the F_2 plants showed that very few of the F_2 plants were wrongly classified. One of them, classed as susceptible (3-4) in the F_2 , produced offspring that segregated; while one plant, classed as intermediate (2-3) in the F_2 , gave rise only to susceptible individuals. Six F_2 individuals, classed as resistant (0-2) and that had given type-2 or 2- reactions, should have been placed in the intermediate group in classifying the F_2 since the progeny in the F_3 lines from these plants segregated. These errors in classification are not surprising when the closeness of reaction of the F_2 plants is taken into consideration.

It is noteworthy that in the F_2 test, conducted in late spring in the greenhouse, heterozygous individuals gave a reaction of type 2-3, intermediate between resistance and susceptibility. In the winter, however, heterozygous F_3 plants were more resistant and gave type-1-2 reactions. Plants, homozygous for resistance and for susceptibility, showed greater stability. The individuals, homozygous for resistance, however, were not all so resistant as the resistant parent, indicating that other factors may play a part in modifying the resistance.

Of the 2466 F_3 plants from 76 segregating lines, 614 gave reactions of type 3 or 4, 1216 a reaction of 1-2, and 636 a reaction of 0 or 0-1. This approximates a 1:2:1 ratio of 616.5:1233:616.5, the deviations being -2.5, -17, 19.5 and $\text{Dev.} \div \text{P.E.}$ 0.17, 1.01, 1.34.

The F_2 and F_3 results indicate that the resistance of Goldfoil C. I. 928 to physiologic race 6 is governed by one main factor.

The 145 F_2 plants whose seedling reactions to mildew had been ascertained were grown to maturity and classified for 2-row and 6-row arrangement. One group included 111 2-row individuals and the other contained 34 6-row plants, which approximates a 3:1 ratio. This is in agreement with studies of other investigators (25, 3, 4) who have found a single-factor difference between 2-row and 6-row forms, the 2-row condition being dominant.

A combination of the data concerning number of rows per head with that obtained for the inheritance of mildew reaction gives the results shown in table 3. The F_2 plants, heterozygous for resistance, are placed in the resistant class, since the heterozygous F_3 individuals from these plants tended, in the winter tests, more toward resistance than susceptibility.

TABLE 3.—*Inheritance of mildew reaction and row number in the F_2 of a cross between Featherston C. I. 1118 and Goldfoil C. I. 928*

Item	2-row		6-row		Total
	Resistant	Susceptible	Resistant	Susceptible	
Observed	84	27	24	10	145
Expected	81.56	27.19	27.19	9.06	
Deviation	2.44	-0.19	-3.19	0.94	
Probable error	4.03	3.17	3.17	1.97	
$\text{Dev.} \div \text{P.E.}$	0.61	0.06	1.01	0.48	

These data indicate a close approximation to the results that would be expected if mildew reaction and row number are inherited independently.

Arequipa C. I. 1256 $\times$ Horsford C. I. 610

The variety Arequipa is awned and Horsford is hooded. Seedling plants of Arequipa give a reaction of type 1-2 to race 6, in the winter. Under similar conditions Horsford gives a type-3-4 reaction. The data concerning the reactions of both F_2 and F_3 seedlings were obtained during the winter months in greenhouse studies.

When the F_2 plants were classified all types of reaction from 1 to 4 were encountered. One hundred and forty-two of the plants gave a reaction of type 3 or 4, and 382 a reaction of 1 or 2. This closely approximates a 1:3 ratio of 131 susceptible:393 resistant, the deviation being 11, and

Dev. ÷ P.E. 1.64. The results indicate that the expression of resistance is due to a single main Mendelian factor.

In order to verify the results obtained in the F₂ generation, F₃ progenies of 25 to 35 plants derived from each of 122 F₂ plants were studied. Four of the F₂ plants were apparently erroneously classified. Twenty-five of the 122 F₂ plants were found to be homozygous for susceptibility, 34 were homozygous for resistance, and 63 were heterozygous for resistance-susceptibility. Of the 1881 F₃ plants from the 63 segregating lines, 491 gave a reaction of type 3 or 4, and 1390 a reaction of 1 or 2. This approximates a 1 : 3 ratio of 470.25 susceptible : 1410.75 resistant, the deviation being 20.75, and Dev. ÷ P.E. 1.64. The results obtained in the F₂ and F₃ indicate that one main Mendelian factor governs the inheritance of the resistance of Arequipa C. I. 1256 to race 6 of the mildew.

The 122 F₂ plants, studied for mildew reaction in the seedling stage, were matured and classified for type of lemma, hooded or awned. Some of the plants bore heads that were hooded like the Horsford parent. Some had the hoods elevated on short awns. The latter probably were heterozygous for the hooded character. Both types were recorded as hooded. Other plants were awned like the parent, Arequipa. Eighty-nine plants were hooded and 33 were awned, which is a close approximation to a 3 : 1 ratio. As shown here and as proved by other investigators (25, 3, 4), the hooded character is dominant. A single pair of factors evidently is involved.

Since the genotypic constitution of the 122 F₂ plants classified for mildew reaction was indicated by the F₃ progeny tests, the F₃ results may be used for classifying the F₂. When these data are combined with those involving the hooded and awned characters, results are obtained as given in table 4.

TABLE 4.—Inheritance of mildew reaction and lemma character in the F₂ of a cross between Arequipa C. I. 1256 and Horsford C. I. 610

Item	Hooded		Awned		Total
	Resistant	Susceptible	Resistant	Susceptible	
Observed	75	14	22	11	122
Expected	68.63	22.87	22.87	7.63	
Deviation	6.37	-8.87	-0.87	3.37	
Probable error	3.70	2.91	2.91	1.80	
Dev. ÷ P.E.	1.72	3.05	0.30	1.87	

Apparently mildew reaction is inherited independently of lemma character.

DISCUSSION

As early as 1902 Marchal (17) showed that the powdery mildew of grasses (*Erysiphe graminis* DC.) comprised a number of physiologic varieties, each

specialized on different grass genera. In 1930 Mains and Dietz (15) reported that the *Hordei* variety contained physiologic races distinguished by the differential reactions of varieties of barley. In the present study the occurrence of 2 additional physiologic races has been demonstrated. These have been designated as races 6 and 7. In order to separate race 6 from race 1, another barley variety, Heil's Hanna 3 C. I. 682, has been added to the list of 4 differentials used by Mains and Dietz. In 1934 Honecker (9) also reported the occurrence of 2 new physiologic races of *Erysiphe graminis hordei* in Germany. Since the reactions of 2 of the 5 differentials to the physiologic races isolated by Honecker are not known these 2 German races have not been included in table 1 of the present report, nor have they been designated by numbers.

The discovery of physiologic races of barley mildew should help to account for some of the discrepancies in the results obtained by early workers. For instance, Marchal (17, (1902)) and Salmon (28) obtained slightly different results when certain species of *Hordeum* were inoculated. It is probable that these investigators worked with different physiologic races. In the present study 5 wild species of *Hordeum* were entirely resistant to race 6. Marchal (17, (1902)) reported positive results on *Hordeum murinum* and *H. jubatum*, and Reed (20) obtained positive results on the first leaves only of *H. nodosum*. It also may be that strains of the host, differing in susceptibility, were used in the various investigations.

In the present study the reactions of varieties resistant in the seedling stage were exceedingly stable despite the fact that certain varieties were slightly more resistant in spring than in winter. Likewise, seedling plants of susceptible varieties were found to give reactions in spring very similar to those recorded in winter for these same varieties.

The effect of environmental factors on the reactions of adult barley in inoculation experiments with mildew in winter and late spring in the greenhouse is well defined. In winter, under conditions of low light intensity and lower temperatures, the varieties susceptible in the adult stage were fully as susceptible as in the seedling stage. Adult plants of varieties resistant as seedlings gave reactions very similar to those recorded in the seedling stage. In spring, however, the adult varieties, susceptible during winter and spring in the seedling stage, were moderately to highly resistant. Adult plants of varieties resistant in the seedling stage were often more resistant than seedlings of the same varieties. Instead of giving 0-1 reactions, as did many of the seedlings, the reactions were type 0. This pronounced resistance of adult plants in the greenhouse in spring may be due to increased light or higher temperatures acting on the host-parasite complex.

Graf-Marin (7) states that he never observed mildew on the leaves of mature barley plants, although seedlings of the same variety developed the

disease. He attributed the resistance of the leaves of adult barley to the fact that the haustoria of the fungus were unable to penetrate the thicker cuticle and walls of the epidermal cells of "old leaves". It should be noted that his conclusions were based on results obtained with only one variety grown in the greenhouse in the spring. It is conceivable that had Graf-Marín inoculated adult plants of this variety in winter, infection would have resulted, as it did on adult plants of susceptible varieties in the investigation here reported. In this connection it also might be noted that Miss Mackie (11) found no excessive morphological differences between leaves of resistant and susceptible barley varieties.

Several investigators (32, 33, 6, 8, 10) have observed that certain growing conditions are more favorable for barley-mildew development and the resistance or susceptibility of the host may be somewhat modified. From the results obtained in the present studies it also is evident that the reactions of some varieties may be modified by environmental factors. This is especially true of adult plants of susceptible varieties as already mentioned. With seedling plants, however, the changes were for the most part not pronounced. This conclusion is supported by the results obtained in the genetical studies.

The "green island" phenomenon, observed in spring on leaves of susceptible varieties in the seedling stage, has been noted by several investigators. Graf-Marín (7) noted "green islands" on barley leaves that had almost been killed by ultraviolet light. Reed (22) mentioned the occurrence of green areas infected with mildew. The yellowing of barley leaves beyond the infected green regions was suggestive of the secretion of toxic substances by the mildew (11). Miss Rice (24) has given a good discussion of the occurrence of this phenomenon in the rusts. In the writer's experiments the "green islands" were occasionally noted on a few leaves that died from causes other than mildew infection. Such "green islands" were very small. The best examples were observed on seedling leaves of some of the susceptible varieties in the spring tests. These leaves generally were fairly heavily infected with mildew and the "green islands" gradually became prominent as the leaf yellowed.

The genetical studies with seedling plants demonstrate that resistance is a definitely inherited character. The resistance of the 3 resistant parent plants studied, Hanna C. I. 906, Goldfoil C. I. 928, and Arequipa C. I. 1256, was shown in each case to be due to a single main Mendelian factor. The resistance of Hanna was incompletely dominant, the heterozygous individuals being somewhat less resistant than Hanna and homozygous resistant segregates. The same was true for Goldfoil. In crosses where Arequipa was the resistant parent, heterozygous individuals were not so clearly differentiated. The resistance of Arequipa is not so stable as that of Hanna or Goldfoil and is more easily varied by environmental conditions and probably is responsible

for the intergradation of the homozygous resistant and heterozygous groups. Honecker (9) in his studies during the winter months also was able to distinguish 3 classes that gave approximately a 1:2:1 ratio. During the summer months, reactions were so modified that individuals, heterozygous or homozygous for resistance, could not be distinguished. In his studies Dietz (5) found susceptibility dominant.

SUMMARY

The reactions of 85 varieties of barley in the seedling stage in greenhouse studies to 2 new physiologic races of *Erysiphe graminis hordei* are given. These 2 races are designated as physiologic races 6 and 7. To the list of 4 differential barley varieties used by Mains and Dietz (15), a fifth variety, Heil's Hanna 3 C. I. 682, was added.

Five wild species of *Hordeum* were highly resistant to physiologic race 6 in tests conducted in winter in the greenhouse.

Seedling barley plants, in winter and spring, have shown no marked changes in reaction at these two seasons to either race 6 or race 7. Certain varieties are slightly more resistant in spring.

Tests of varieties in the adult stage in greenhouse studies, have shown that such barley plants, in spring, are more resistant to mildew than seedling plants of the same varieties. Adult plants in winter are fully as susceptible as seedling plants of the same varieties.

Studies of F_2 and F_3 of 3 crosses between resistant and susceptible plants indicate that resistance or susceptibility to physiologic race 6 of barley mildew in the seedling stage is inherited in definite Mendelian proportions. (1) In the cross, Svansota M786 $\times$ Hanna C. I. 906, a single pair of factors is involved. Resistance is incompletely dominant. (2) In the cross, Featherston C. I. 1118 $\times$ Goldfoil C. I. 928, a single pair of factors is involved. Resistance is incompletely dominant. The reactions of heterozygous individuals were altered by environmental factors. Independent inheritance of the factor pairs for resistance versus susceptibility, and 2-row spikes versus 6-row spikes is indicated. (3) In the cross, Arequipa C. I. 1256 $\times$ Horsford C. I. 610, a single pair of factors is involved. Resistance is dominant. Independent inheritance of the factor pairs for resistance versus susceptibility and hoods versus awns is suggested.

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